

# Evidence for genetic monogamy and female-biased dispersal in the biparental mouthbrooding cichlid *Eretmodus cyanostictus* from Lake Tanganyika

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## Abstract

In this study, we investigate whether apparent social monogamy (where a species forms a pair bond but may participate in copulations outside the pair bond) corresponds with genetic monogamy (where individuals participate only in copulations within a pair bond) in a biparental mouthbrooding cichlid fish, *Eretmodus cyanostictus*, from Lake Tanganyika, Africa. Our findings suggest that *E. cyanostictus* is both socially and genetically monogamous and that monogamy may result from limited opportunities for polygyny, rather than from reproductive benefits of monogamy. Mating systems are believed to influence the relative rate of dispersal of the sexes, and our results suggest that *E. cyanostictus* displays female-biased dispersal, providing some support for the ‘resource competition’ hypothesis driving sex-biased dispersal.

Keywords: Cichlidae, Eretmodine, mating systems, microsatellites, sex-biased dispersal

## Introduction

The study of animal mating systems has been revolutionized over the last decade by the development of the DNA-based techniques for parental assignment (Longmire et al. 1992; Leisler & Wink 2000), and this has revealed hitherto unexpected complexity in the mating systems of many taxa. For example, 30 years ago monogamy was accepted as the predominant mating system for birds. It is now recognized that genetic monogamy is the exception rather than the rule: less than 10% of socially monogamous birds (where pair bonds are formed but copulations outside the pair bond may occur) also show genetic monogamy (where there are no copulations outside the pair bond) (Birkhead & Møller 1998; Morell 1998). Genetic monogamy also appears rare in fishes and to our knowledge has been documented only twice before: in the internally fertilizing seahorse *Hippocampus subelongatus* (Jones et al. 1998; Kvarnemo et al. 2000) and in the externally fertilizing large mouth bass (*Micropterus salmoides*) (DeWoody et al. 2000).

Monogamy is expected if two individuals are needed to (1) effectively feed, incubate or guard young (Lack 1968; Barlow 1984); (2) guard a territory (Barlow 1984); or (3) because mate availability is low (Ghiselin 1969; Brotherton & Rhodes 1996). These factors do not seem to apply for *Eretmodus cyanostictus*, a small, socially monogamous, biparental mouthbrooding cichlid fish, from Lake Tanganyika, Africa. Females initially brood small clutches in their buccal (mouth) cavities, before transferring them to the male, who broods them until release (Kuwamura et al. 1989). Monogamy does not appear to be maintained by the need to defend young jointly — parents do not defend newly released young, and each sex is capable of incubating the entire clutch orally until maturity (Morley 2000). Nor does monogamy appear to be maintained by the need to defend territories jointly — single individuals can retain their territories after experimental removal of one member of a breeding pair (Morley & Balshine 2002). Moreover, a low density of potential partners is unlikely to maintain monogamy, as individuals gained new partners quickly following experimental removal of male or female mates (Morley & Balshine 2002). In cichlid fishes, biparental mouthbrooding is thought to be an intermediate and

unstable stage between biparental substrate guarding and maternal mouthbrooding (Barlow 1963; Goodwin et al. 1998) and, consequently, the persistence of social monogamy remains a mystery in this species. The first aim of this study is to investigate whether social monogamy (assumed from behavioural observations on *E. cyanostictus*) translates to true genetic monogamy.

The genetic mating system may also have important implications for the relative rates of dispersal of each sex. Male-biased dispersal has been demonstrated previously in a polygynandrous cichlid fish from Lake Malawi (Knight et al. 1999). Three hypotheses suggest that male-biased dispersal will occur in polygynous species. These are: (1) the 'resource-competition hypothesis' (Greenwood 1980), that states that the philopatric sex will be the one that benefits most from a familiarity with its natal area; (2) the 'local mate competition' hypothesis (Perrin & Mazalov 2000) which suggests that individuals disperse to avoid competing (for mates) with relatives, thus increasing their inclusive fitness; and (3) the 'inbreeding avoidance hypothesis' (Pusey 1987; Perrin & Mazalov 2000), which suggests that the sex incurring the greatest cost from inbreeding will disperse. In monogamous species, female-biased dispersal is predicted by the 'resource competition' hypothesis. Males are likely to benefit more than females from familiarity with birth site as they help to rear young, and need to acquire and defend a territory with sufficient resources to attract a female (Favre et al. 1997). No bias is predicted in monogamous species by the inbreeding avoidance or local mate competition hypotheses. Therefore, if *E. cyanostictus* are genetically monogamous, we would expect either a female bias in dispersal, providing support for the resource competition hypothesis, or no bias in dispersal, providing evidence for the inbreeding or mate competition avoidance hypotheses. We predict male-biased dispersal if cuckoldry is common. To investigate whether a sex-bias in dispersal exists in *E. cyanostictus* and its direction (if any), we compared the degree of relatedness between pairs of males and females in the field.

## Materials and methods

### Sample collection

The field study was conducted in an area (100 m<sup>2</sup> at 3 m depth) on the southern shore of Lake Tanganyika, northwest of Mpulungu, Zambia in Kasakalawe Bay, 100 m east of Kasakalawe Village. Pairs of *E. cyanostictus* were identified by swimming along a transect line in the study area, and a numbered rock was positioned on each pair's territory boundary. All fish were identified reliably by their location and the unique pattern of blue spots on their body. Behavioural observations with scuba were conducted on pairs each week from 4 February to 14 April 1998. Detailed

descriptions of the site, pair identity and the behavioural watches can be found elsewhere (Morley 2000; Morley & Balshine 2002). In mid-April 1998, 13 adult pairs and their entire clutches, a single brooding adult male and one additional adult pair without a clutch, were caught using monofilament nets. In total 203 eggs and fry, as well as 14 adult females and 15 adult males, were collected for this study. Fin clips from both parents and the entire clutches (whole eggs or fry) were preserved in 95% ethanol.

### DNA preparation and amplification

Total DNA was extracted from eggs/fry and fin clips using proteinase-K digestion followed by the Bilatest magnetic bead extraction kit (Bilatest AG, Germany), using the Roboseq 4204 S robot (MWG). Extracted DNA was resuspended in 100 µL of Sigma tissue culture water (Sigma-Genosys).

### Microsatellite amplification

All offspring and adult samples were screened for variation at each of three SSR loci, one of which is a perfect dinucleotide repeat (Pzeb1, van Oppen et al. 1997), one is an imperfect dinucleotide repeat (TmoM25, Zardoya et al. 1996) and one is a compound repeat (TmoM5, Zardoya et al. 1996). Adults were screened at two additional loci, UNH002 (Kellogg et al. 1995) and Pzeb3 (van Oppen et al. 1997), both of which are perfect dinucleotide repeats. Polymerase chain reactions (PCRs) were performed in a MJ Research PTC-200 thermal-cycler under the following conditions: 94 °C, 120 s, followed by five cycles of 94 °C, 45 s; A °C, 45 s; 72 °C, 45 s, followed by 30 cycles of 91 °C, 30 s; A °C, 30 s; 72 °C, 30 s, followed by 72 °C, 10 min. The annealing temperatures (A) are given in Table 1. Ten µL reaction mixes consisted of 1 µL (≈ 20 ng) template DNA, 0.5 µm of each primer, 200 µm of each dNTP, 0.26 units Taq polymerase (Bioline), 1 µL 10 × reaction buffer (Bioline) and 1.5 mm magnesium chloride. Amplified products were resolved on an ABI 377 automated sequencer (Applied Biosystems). genescan and genotyper software (Applied Biosystems) were used to size the fragments.

### Data analysis

Pop100gene (<http://www.montpellier.inra.fr/URLB/pop100gene/pop100gene.html>) was used to estimate allele numbers, and observed and unbiased expected heterozygosities at each locus. cervus 2.0 (Marshall et al. 1998) was used to calculate overall exclusion probabilities (the expected proportion of individuals in the population that would be rejected as parents of an offspring given that the maternal genotype was known) for the three loci. Pairwise relatedness (R) was estimated for the adult samples using five microsatellite loci with the program relatedness

Table 1 The five microsatellite loci used for genetic analysis. Expected ( $H_E$ ) and observed ( $H_O$ ) heterozygosities were estimated using the popgene computer program (available at: <http://www.montpellier.inra.fr/URLB/pop100gene/pop100gene.html>)

Locus	Label	A	N	No. of alleles	Min	Max	$H_O$	$H_E$
Pzeb1	FAM	55	29	11	129	154	0.72	0.84*
TmoM25	HEX	60	29	11	337	365	0.86	0.85
TmoM5	FAM	55	29	25	315	377	0.79	0.92
Pzeb3	HEX	55	29	4	318	324	0.28	0.30
UNH002	HEX	52	29	16	161	205	0.86	0.82

A = PCR annealing temperature, N = no. adults typed, min = minimum allele size, max = maximum allele size. \*Significant deviation from Hardy–Weinberg equilibrium before (but not after) Bonferroni correction.

5.08 (Queller & Goodnight 1989). Separate matrices of pairwise relatedness were produced for 15 males and 14 females and the average relatedness of each individual to all other individuals of the same sex calculated [this reduces the effects of pseudoreplication (Knight et al. 1999)]. A two-sample permutation test [rundo 1.0, (Jadwiszczack 2002)] was then performed to test for a difference in average relatedness between males and females. Permutation tests combine all data, randomly assign data to groups (male and female in this case), and then calculate the difference between the mean of the two groups. This is repeated N times (10 000 in the current study) and exact P-values obtained by comparing the difference between the means of the real data with the frequency distribution obtained from the permuted data.

## Results

All the observational data suggested that *E. cyanostictus* was socially monogamous (Morley 2000). Thirteen adult pairs and their entire clutches, a single male with his clutch, and one additional adult pair without a clutch were genotyped. Only one member of each pair was found to be carrying eggs or young in their mouths. The mean number of offspring carried by individuals was 14.5. For the adult samples, the number of alleles per locus ranged from four in Pzeb3 to 25 in TmoM5. Unbiased expected heterozygosity ( $H_E$ ) ranged from 0.30 in Pzeb3 to 0.92 in TmoM5 (Table 1). The total exclusionary power for the three loci combined was 0.98.

Of the 14 clutches genotyped, 202 individuals displayed genotypes consistent with their having been sired by the assumed father. A single individual (the 203rd individual) showed an allele inconsistent with either parent at locus TmoM5. As the other two loci were consistent with the parental genotypes, we assume a mutation occurred at a

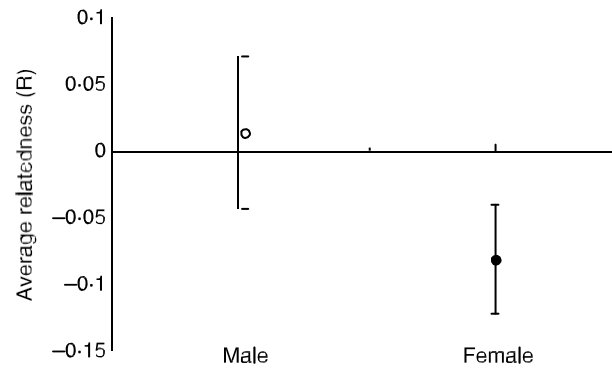


Fig. 1 Average pairwise relatedness of each male to all other males (no. males = 15) vs. average pairwise relatedness of each female to all other females (no. females = 14) in a population of *E. cyanostictus*. Error bars are standard deviation.

single allele in a single locus in this individual, resulting in a reduction in allele size from 133 to 131 – a single repeat unit. Spontaneous mutations have been documented in other parentage studies (Jones et al. 1999; McCoy et al. 2001). Therefore, we concluded that all 14 clutches showed genotypes consistent with a single pair of parents – no more than four alleles per locus.

## Evidence for sex-biased dispersal

The average pairwise relatedness of each individual to all other individuals of the same sex ranged between  $-0.094$  and  $0.013$  for males and  $-0.0041$  and  $-0.177$  for females. Males were found to be significantly more closely related on average [mean  $\pm$  standard deviation (SD) =  $0.013 \pm 0.057$ ] than were females (mean  $\pm$  SD =  $-0.0817 \pm 0.04$ ) (two-sample permutation test, 10 000 randomizations, two-tailed  $P < 0.0001$ , Fig. 1).

## Discussion

### Maintenance of monogamy

We genotyped all offspring from 14 clutches, and the genotypes of each clutch were consistent with having been sired by a single male and female. Thus, the results of this study indicate *E. cyanostictus* is genetically and socially monogamous.

The tribe Eretmodini consists of four nominal species in three genera. *E. cyanostictus* and *Tanganicodus irsacae* are biparental mouthbrooding species, while *Spathodus marlieri* and *S. erythron* are maternal mouthbrooding species. Biparental mouthbrooding is thought to be derived from biparental substrate guarding, and intermediate to uniparental mouthbrooding (Barlow 1963; Gittleman 1981; Balshine-Earn & Earn 1998; Goodwin et al. 1998). The

reasons why biparental mouthbrooding has persisted in two of the three genera remain obscure. Female *T. irsacae* can brood offspring to a viable size without the help of the male (Kuwamura et al. 1989), and this also is the case for *E. cyanostictus* (Morley 2000).

There are various factors that may favour the maintenance of monogamy in *E. cyanostictus*. First, the male-biased sex ratio (Morley & Balshine 2003) might make it difficult for males to find additional mating partners if they desert females after spawning (although females could desert males after transferring their broods). Second, *E. cyanostictus* retains only a vestigial swim bladder (Brichard 1989), which allows it to 'sit' on the substrate and avoid battering by wave action. Prolonged swimming, which is necessary when searching for new mates or territories, may be considerably costly compared with fish species with functioning swim bladders. Third, laboratory experiments suggest that both sexes guard their mates and repel intruders, reacting more strongly to same-sex than opposite-sex intruders (Morley 2000). These findings suggest that monogamy may occur in *E. cyanostictus* because of constraints on polygyny for both sexes rather than benefits to monogamy itself. This also appears to be the reason for monogamy in particular bird species (Krebs & Davies 1983; Piper et al. 1997).

#### Evidence for sex-biased dispersal

The data from this study suggest that females disperse more than males in *E. cyanostictus*, which is the opposite situation to that found in a polygynandrous cichlid from Lake Malawi (Knight et al. 1999). Several hypotheses may shed light on the female biased dispersal in this genetically monogamous, rock-dwelling cichlid. Inbreeding avoidance (Bengtsson 1978; Parker 1979; Waser et al. 1986) may be important, as significant genetic structure is evident on a continuous rocky shoreline not divided by physical barriers, suggesting that *E. cyanostictus* are poor dispersers (Taylor et al. 2001). Theory predicts that the sex that incurs the highest cost of inbreeding should be the dispersing sex (Perrin & Mazalov 1999). However, in genetically monogamous mating systems, such as *E. cyanostictus* (see above), the cost of inbreeding should be identical for males and females, as both would be forced to accept a single inbred mating opportunity at the expense of a single outbred mating opportunity. There should be no asymmetry in inbreeding costs in monogamous species, and no sex-bias in dispersal, assuming equal sex-ratios. Therefore, we would expect no sex-bias in dispersal if inbreeding avoidance plays a significant role in driving dispersal in *E. cyanostictus*.

The 'local mate competition' hypothesis also predicts no bias in dispersal in monogamous systems as both sexes are equally affected by local mate competition. Hence our data

of female biased dispersal do not provide support for this hypothesis.

The 'resource competition hypothesis' (Greenwood 1980) focuses on the relative advantages of philopatry for each sex, and predicts that the philopatric sex will be the sex that benefits most from a familiarity with its birth site. *E. cyanostictus* males may best enhance their own fitness by defending a high quality territory that attracts females and provides high quality resources (food and shelter) for the offspring. If males take a significant responsibility in acquiring and defending the breeding territory, then the advantages of philopatry will be greater for male *E. cyanostictus* than for females. Currently we do not know which sex acquires the breeding territory, although males do defend the territory more vigorously than females (Morley & Balshine 2003). More research is now needed to investigate the hypothesis that female-biased dispersal is a result of the benefits of philopatry for males.

This study is based on a limited set of samples collected from a single population, and consequently any conclusions drawn from the data must be treated with some caution. While the population sampled in this study appears to be genetically monogamous and to exhibit female-biased dispersal, we highlight that other populations may exhibit different behavioural characteristics.

In summary, *E. cyanostictus* appears to be both behaviourally and genetically monogamous. Such monogamy may be maintained through constraints on polygyny rather than advantages to monogamy, and in contrast with polygynandrous cichlids, *E. cyanostictus* displays female-biased dispersal.

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